Third, whatever turns out to be the environmental cue to which leaves of *B. trifoliata* respond in their development, the plant offers potentially fertile material with which to examine the details of leaf development. One thinks back to the early studies of leaf development, where simple manipulations of the growth environment of cuttings provided the first indications of the importance of both hormonal control and positional effects as well as the external environment on leaf differentiation, such as moisture availability, light intensity and day length (reviewed in [10]). Experiments along these lines, with attention directed at both the abiotic environment experienced by leaves as well as the influence of nearby foliage, would be a good place to start.

Our first response in seeing the photographs of *B. trifoliata* leaves paired with those of its various hosts will perhaps be incredulity, not so much because of scepticism about the adaptive value of the crypsis they show, but because of the absence of any sufficiently plausible hypothesis for an underlying proximate mechanism. In the absence of evidence for a plausible mechanism, the publication seems premature. But plants do wondrous things, and ultimately it is exciting to read Gianoli and Carrasco-Urra's [1] paper, which seems sure to prompt further work. In this context, it is worth recalling the early scepticism directed towards Barbara McClintock's jumping-gene hypothesis [11]. One is also reminded of Darwin's assessment of the inventiveness of natural selection when considering the evolution of orchids [12]:

> The more I study nature, the more I become impressed […] that the contrivances and beautiful adaptations [acquired through natural selection] transcend in an incomparable degree [those] which the most fertile imagination of the most imaginative man could suggest with unlimited time at his disposal.

The advantages gained through the ability of plants to respond plastically to the opportunities and dangers in their environment, given their inability to move, is easy to accept in general. But the discovery of a plant that can evidently interpret and respond to its local biotic environment as precisely as does *B. trifoliata* would seem to fall into the category of adaptation capable of inspiring the awe to which Darwin was here referring.

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Department of Ecology and Evolution, University of Lausanne, 1015 Lausanne, Switzerland.
E-mail: john.pannell@unil.ch

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Habitat Complexity: Coral Structural Loss Leads to Fisheries Declines

Direct human impacts and global climate change are altering the composition and structure of coral reef habitats. These changes are simplifying size–abundance relationships of reef fish communities, reducing productivity through the system and ultimately threatening fisheries yields.

Nicholas A.J. Graham

The physical three-dimensional structure (or structural complexity) of many ecosystems is created by foundation species, such as trees, corals, and giant kelp. The structural complexity provided by these organisms contributes substantially to the biodiversity and productivity of these ecosystems — kelp structure, for example, provides habitat for a wide range of fishes and marine invertebrates [1]. However, human activities are threatening foundation species, which has dire implications for the maintenance of biodiversity and ecosystem processes. The loss of foundation tree species, for example, can lead to reduced nutrient flux, carbon sequestration and energy flow in forests [2]. How reductions in foundation species will influence the goods and services that ecosystems provide to humans is poorly understood. In this issue of *Current Biology*, Alice Rogers, Julia Blanchard and Peter Mumby [3] show that there could be a three-fold reduction in fisheries productivity on coral reefs through the loss of the physical habitat structure provided by reef corals.

Reef-building corals are critical foundation species on coral reefs, creating a complex three-dimensional structure that offers niche space for a wide array of other organisms. This structural complexity is, in part, responsible for the high biodiversity and productivity of coral reef ecosystems in what would otherwise be unproductive areas of the ocean. However, the very foundational species of the ecosystem are also turning out to be its Achilles heel.

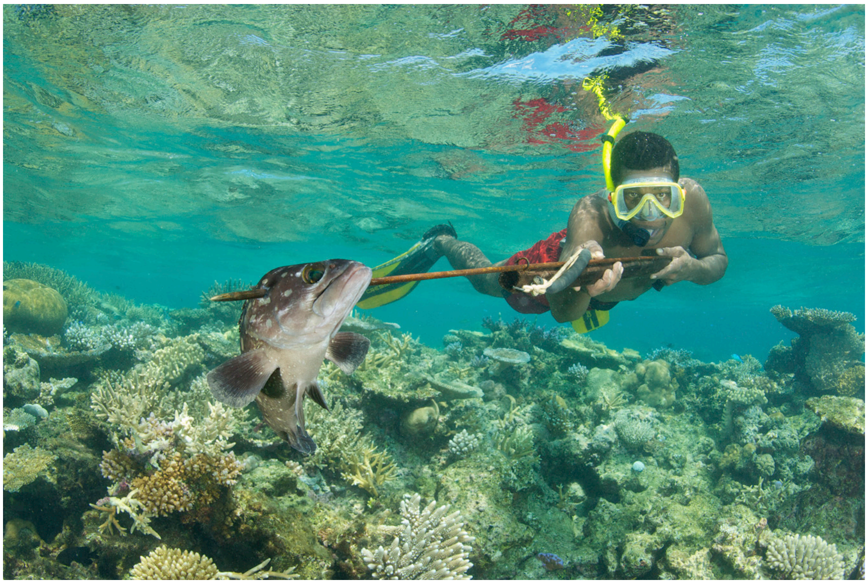

Figure 1. A spear fisher with his catch on a coral reef in Fiji.
Coral reef habitats with high structural complexity are important for fish productivity and maintaining fishery yields to coastal people. Photo: Keith A. Ellenbogen.

Despite the relatively stable composition of coral reefs in the geological record at least as far back as through the Pleistocene [4], reef corals are proving extremely vulnerable to a wide range of escalating direct and indirect human impacts. For example, extensive mortality of corals has been documented due to climate change driven coral bleaching, land based nutrient influxes, fishing, and tropical storms.

With the loss of live coral cover also comes a loss of reef structural complexity. Evidence for declining complexity has been found on coral reefs in the Indo-Pacific and Caribbean Sea [5,6]. Reductions of reef structure following disturbances have led to demonstrable effects on the wider ecosystem, such as reduced abundance and diversity of reef fishes [7]. With the importance of structural complexity increasingly recognized, assessments of the relationships between structural complexity and the wider ecosystem have become ever more sophisticated. For example, while it has long been known that fish associate with refuges within the reef structure that correspond to their body size [8], recent work has shown that the relationship between abundance and fish body depth is multimodal, and the peaks in abundance correspond to high availability of habitat structure of specific sizes [9]. Despite this increased understanding of the importance of habitat structure at different scales, it has been hard to pin down the implications of changing reef structural complexity and associated fish communities for human societies.

One of the strongest links between coral reefs and human societies is through fishing (Figure 1). Coral reefs support around a quarter of all small-scale fisheries globally, with ∼6 million people directly engaged as fishers and many millions more dependent on the resource through other livelihoods or for food [10]. There are indications that climate change or other threats to reefs may negatively impact fishing yields on coral reefs [11]. For example, loss of structural complexity has been shown to cause declines in smaller bodied species of fish and smaller size classes of larger fish, which has been hypothesized to lead to longer-term reductions in fishing yields [5]. However, it has remained difficult to directly link reduced reef structural complexity to changes in fish productivity.

Part of the challenge of linking changes in reef structure to fishing yields is the complexity of coral reef social-ecological systems. These fisheries have proved incredibly difficult to assess, as they typically target many species of fish, use multiple types of fishing gear, and are often in countries with weak or missing research and management institutions. This has led to calls for simple community-scale indicators for the status of a fishery. One such community metric that has gained a lot of traction is size spectra analysis. This metric assesses the state of a fish community based on the relationship between fish body size and abundance, regardless of species identity. The approach has proved powerful in temperate ecological and fisheries research, for example helping to predict unfished baseline production and trophic structure in marine consumer communities [12] and to understand size-based trophic coupling between predators and detrital feeders [13]. Although size spectra analysis has been applied to coral reefs [5,14], the wide utility of the approach remains under-explored.

Rogers *et al.* [3] pull together several of these key areas of research and theory (importance of structural complexity, availability and influence of structure across scales, and size spectra analyses) in an innovative way, to help illuminate the mechanism by which declining structural complexity reduces fishing productivity. The authors link availability of habitat structure to size spectra analysis, finding much more complex, non-linear, relationships in the slope of body size and abundance in fish communities from areas where habitat structure is more complex. These non-linear size-abundance patterns reflect disproportionately higher abundances of fish of small to medium size, potentially enhancing the flow of energy, or production, through the system.

The authors go on to parameterize a size-structured food web model that has been previously applied to structurally simple habitats in the North Sea [13]. Outputs from the basic model, parameterized for coral reefs, provided a good fit for fish communities from low complexity reef habitats. Simulating habitat structure availability, the model produced non-linear body size–abundance relationships, similar to those observed from complex reef habitats. Importantly, the authors were able to model differences in the flux of biomass through fish size classes, which is directly related to fisheries productivity, in response to changes in structural complexity. The model indicated that a substantial loss of structural complexity (such as that inferred from the two habitat contrast in their empirical data) can lead to a three-fold reduction in fisheries production [3]. Given widespread degradation of coral reef habitat in many parts of the world, including a loss of structural complexity, such results are worrisome. The findings provide an important mechanistic basis to estimate likely changes in fisheries productivity through varying loss of habitat structure.

This study opens up many avenues for both future research and applications to resource management initiatives. Maintaining structural complexity or encouraging it to re-build, for example by managing important ecosystem processes, is a formidable challenge for coral reef managers and resource users. Some areas of reefs are more robust than others, with the underlying reef matrix providing stable structural complexity. Careful management of these stable areas may be important, although long-term stability may be difficult to predict in such dynamic systems. Importantly, ecological feedbacks can promote recovery of corals following disturbances—for example, adequate grazing by herbivorous fish species can prevent algal proliferation and allow successful coral recruitment and survival [15]. This indicates that careful stewardship of key functions played by reef fishes will be critical to the long-term maintenance of reef structure and productivity.

Many coral reefs are changing in composition due to differential vulnerability and recovery potential of corals and other organisms to various human impacts [16]. How these novel ecosystem compositions will influence availability of refuge space for fishes and drive fisheries productivity from coral reefs will require a substantial amount of research. A part of this future research agenda should focus on empirically derived quantification of habitat structure at differing scales to better understand and parameterise inputs to production models such as the one developed by Rogers *et al.* [3].

The empirical data used by Rogers *et al.* [3] came entirely from a large, long-established and high compliance marine reserve in the Bahamas. The extent to which structural complexity influences fisheries productivity under chronic fishing pressure remains uncertain, because a wide range of fish sizes can be targeted, with implications for ecological interactions. Such knowledge will be critical because fishing is a pervasive driver of coral reef fish communities, and in the majority of countries marine reserves protect only a fraction of the total reef area [17]. Understanding the net benefit in productivity of high structural complexity in fished seascapes will be of critical importance to management actions, such as phasing out fishing gears that damage habitat or that capture fish species with important ecological roles [18].

The link between coral reef decline and loss in fishing productivity has substantial consequences for the millions of small-scale fishers dependent on coral reefs, further emphasising the need for improved understanding of linked social-ecological systems for coral reefs. This may include identification of differential vulnerability of coastal communities and adjacent ecosystems to climate impacts [19], or the capacity for coastal communities to adapt in response to declines in fisheries yields [20]. A better understanding of linked social-ecological coral reef systems will not only enable impacts to be better assessed, but will also greatly increase the number of possible solutions to sustainably manage these important ecosystems and their associated fisheries.

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ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland 4811, Australia.
E-mail: nick.graham@jcu.edu.au

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